

## ACTIVE BRANCHIAL AND RAM GILL VENTILATION IN FISHES<sup>1</sup>

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Fish biologists have long known that adult mackerel and tunas (Scombridae) can be kept alive only in tanks of a shape and size that permit continuous swimming at speeds just over  $1 \text{ km} \cdot \text{hr}^{-1}$ . Hall (1930) dramatically demonstrated the physiological basis for this observation in 1930. He found Atlantic mackerel, *Scomber scombrus*, slowed in swimming by towing erlenmeyer flasks could not maintain normal blood-oxygen saturation values as could unimpeded fish. These results and the absence of visible ventilation movements in adult swimming mackerel led him to conclude that open-mouth swimming (ram gill ventilation) is routine for this fish, and that the ability to effectively ventilate gills by mouth and opercular pumping had been lost.

Now it is known that other pelagic and mid-water fishes can readily suspend active breathing when on the move at velocities about  $1.5 \text{ km} \cdot \text{hr}^{-1}$  or higher and also resort to ram ventilation of the gills (Muir and Buckley, 1967, remora; Smith, Brett and Davis, 1967, sockeye salmon; Roberts, 1970, 1974, four marine species). Yet these other fishes, unlike scombrids, retain the ability to ventilate at rest in the water column or when maneuvering at slow speed. In other words, the mackerel-like fishes seem to have "outgrown" the capacity of their active ventilatory systems (buccal and opercular pumps) to oxygenate the blood as adults so that continuous swimming becomes a survival necessity.

Many factors tied to the life styles evolved by different lines of fishes played significant roles in the development of the ability to transfer from active to ram gill ventilation when swimming speed picks up from rest (Hughes, 1960a; Hughes and Shelton, 1962). Most crucial must have been the relatively higher metabolic cost of oxygen uptake from water compared to air; a cost largely due to the low solubility of oxygen and the work of pumping water, a respiratory medium of high viscosity and density (Hughes and Roberts, 1970; Randall, 1970b). Consequently, it seems decidedly of advantage for a good swimmer to switch from active to ram ventilation as it grows to a size at which it can routinely cruise fast enough to overcome gill flow resistance, but still ensure complete blood oxygenation. This analysis substantiates this view with detailed and updated experiments. A brief resumé of these was reported earlier (Roberts, 1970).

### MATERIALS AND METHODS

Experiments were completed with the five species of fishes listed in Table I. They were obtained by trapping in Buzzards Bay by the aquarium staff, National

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TABLE I  
*Species used to determine swimming velocities for conversion  
 from active to passive gill ventilation*

Species	N	Standard length, cm (range)	Weight, g (range)	Experimental temperature, °C
Atlantic mackerel <i>Scomber scombrus</i>	5	19.1 (15.8–20.0)	71.9 (43.0–83.3)	18.5–22.0
Blue runner <i>Caranx crysos</i>	7	19.2 (17.6–20.5)	153.3 (114–178)	18.5–19.5
Bluefish <i>Pomatomus saltatrix</i>	11	19.3 (17.5–22.0)	105.2 (62.9–141)	16.0–19.5
Northern scup <i>Stenotomus crysops</i>	5	17.2 (14.5–18.5)	102.4 (72.2–115)	19.5–20.0
Striped mullet <i>Mugil cephalus</i>	4	20.5 (19.3–21.4)	101.7 (90.6–110)	20.0–20.5

Marine Fisheries Service, Woods Hole, Massachusetts, or by bait and lure casting off the stone jetty in Woods Hole Harbor. The blue-runners, scup, and mullet were young adults of smaller than average size. The mackerel and bluefish juveniles were of a size commonly called "tinker" mackerel and "snapper blues." Except for the mackerel that were used soon after capture at the capture temperature, the fish were kept in the large holding tanks of the aquarium in running sea water. To some extent, the experimental and holding temperatures were seasonally dependent. Most of the experiments were done during summer months and continued into late fall as the sea-water temperature at the laboratory intake warmed from 14 to 22° C (August) and fell again to about 12° C (December). In all cases, the experiments were done either at the intake temperature or at higher temperatures maintained by mixing of "raw" intake water and warmed sea water from the large reservoir in the recirculating system of the aquarium. During holding periods the fish were fed daily on diced herring and soft-shell clams.

Since completion of studies at Woods Hole for species listed in Table I, preliminary results to be reported elsewhere have been obtained using similar procedures. These results are included in Table III (Roberts, unpublished) and in the discussion. The report on the sand tiger shark given in Table III was based on repeated visual inspection of a single specimen swimming in the large display tank at the aquarium at Woods Hole. Remarks on non-ventilating rockfish apply to the blue rockfish, *Sebastes mystinus*, the olive rockfish, *Sebastes serranoides*, and the bocaccio, *Sebastes paucispinis* taken at Tanner Bank near San Clemente Island, California.

#### *Activity recording during swimming*

*Swimming apparatus.* The fish were made to swim against a pump stream in a version of the swimming chamber used by Sutterlin (1969) in order to determine critical swimming velocities for transitions from active to passive gill ven-

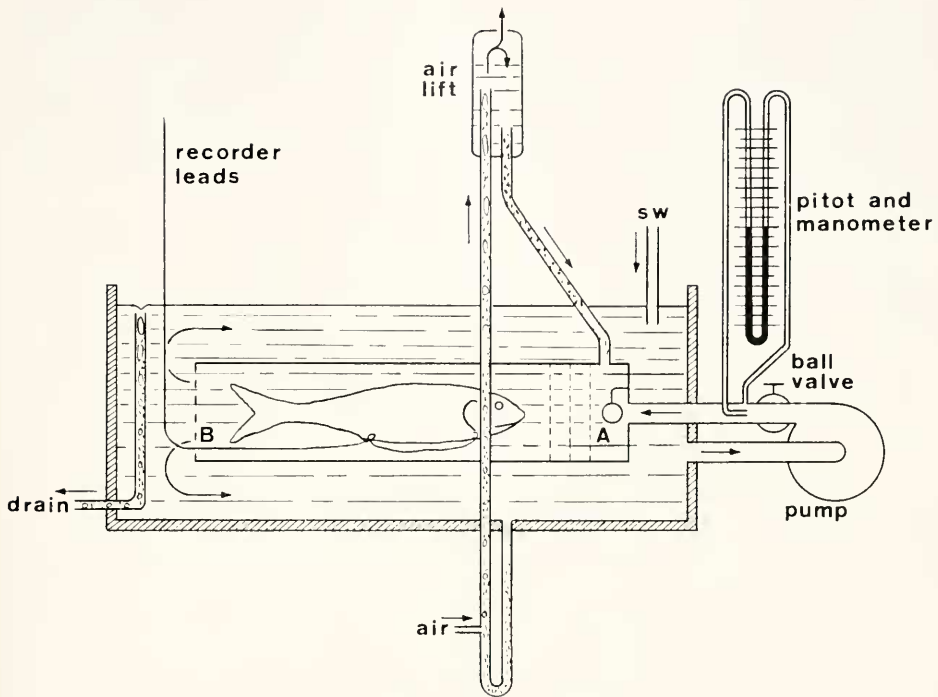


FIGURE 1. Diagrammatic representation of the swimming tunnel used. Design features are similar to those of Sutterlin (1967) with the addition of the air lift circulator for maintaining a slow velocity flow through the tunnel, and fitting around the outer chamber of a 1/4 inch-mesh galvanized Faraday cage. The symbols *A* and *B* represent respectively, the front ball spreader and flow screens, and the rear retainer screen (see text). Temperature control was obtained by use of a thermoregulator-heater located in the outer bath and operated at a set point higher than the entering sea water (*sw*).

tilation (Fig. 1). The centrifugal pump (neoprene body and impeller) of 1/3 hp produced flow velocities up to  $90 \text{ cm} \cdot \text{sec}^{-1}$  in the plexiglas swimming tube (78.5 mm ID) by control of a PVC ball-valve located between the pump outlet and the pitot flow meter. Microturbulent flow and a uniform front were maintained by a ball "spreader" and three, 16-mesh stainless-steel screens at the front of the swimming tube. The rear end of the tube was fitted with a coarser screen of 6-mesh to confine the fish within the tube and to permit free movement of the electrode cable trailing from the fish as it changed its position in response to changes in flow velocity.

*Calibration of flow velocity.* The pitot flow-meter was calibrated indirectly because the flow relationships between the inflow tube from the pump and the swimming chamber proved to be non-linear largely due to back-pressure effects of the spreader ball and the three front screens. Two methods were used that gave similar flow rates for given deflections of the mercury manometer (tubing spaces, water filled). For the first method, slugs of methylene blue dye injected into the pump intake were timed as they passed between the last flow-control

screen at the front, and the rear screen of the swimming tube. The second method (Sutterlin, 1969) was used with the bath filled with fresh water and depended upon timing conductance changes in the stream flow between the electrode pairs located in the walls of the swimming tube, front and rear, as small amounts of saturated KCl, injected into the pump intake, passed the electrodes. Corrections for fish displacement were not made for the cross-sectional area of the fish seldom exceeded 1/10 of the swimming tube.

*Electrode placement and activity waveforms.* Each fish was anesthetized in MS 222 solution ( $0.1 \text{ g} \cdot \text{l}^{-1}$ ) for insertion of electrode pairs for recording waveforms of muscle action potentials related to respiratory and cardiac cycles (Roberts, 1964; Sutterlin, 1969; Spoor, Neiheisel and Drummond, 1971). Electrode pairs were made up of lapwound, 1-m lengths of 45 gauge, insulated stainless-steel wire (Johnson, Matthey and Co., Ltd., England, annealed, epoxy coated) with bared and hooked tips threaded through 22 gauge syringe needles. These were inserted, one pair into the pericardial space, and the other into one of the ventilatory muscles, usually the *adductor mandibularis*. The needles were withdrawn after electrode placement, and the wires secured by skin ties at the insertion site and again at the anal opening. In this way, looping of the formed cable around the tail and tangling was minimized after recovery of the fish in the swimming tube. When tail-beat frequencies were to be recorded (*e.g.*, mullet), *mu*-metal bands (high magnetic permeability) were wrapped around the caudal peduncle for proximity detection of lateral tail movements. A detector coil with permanent field magnets was fitted around the outside of the swimming tube for this purpose. It was made up by winding 38 gauge enameled magnet wire around a coil form incorporating eight Alnico bar magnets (6 mm by 48 mm long, spaced 20 mm: 4 each side). The magnets were oriented parallel to the tube axis with like polarity (north to north) on each side, but opposite in polarity between the two sides, in order to maximize the horizontal magnetic flux density across the tube. The finished coil form was potted in epoxy resin to form a loose fitting, short cylinder. The lead cable incorporated a two-stage RC filter to reduce 60 cycle interference. Distortion of the field by the moving tail band of *mu*-metal generated an AC signal at the tail-beat frequency adequate for polygraph recording at a gain level of 10 to  $50 \mu\text{V} \cdot \text{mm}^{-1}$ .

Usually it was possible to record waveform of both cardiac and ventilatory cycles on a single channel of the R-series Dynographs used (Beckman Instruments, Inc.). This was done by trial-and-error combination of the four electrode leads in the trailing cable, and by appropriate adjustments of the band-pass filters on the input couplers of the polygraph. When clear differentiation of the two waveforms was not possible on one channel, or when tail-beat frequencies were desired, two recording channels were used (*e.g.*, Fig. 4, mackerel and mullet). Usually, the high frequency components of the EMG (electromyogram) signals were suppressed by band-pass control so that only the slow wave part of the signal was displayed by the pen writer. This was done usually to enable differentiation of ECG (electrocardiogram) and EMG waveforms on a single record channel.



*Training and experimental procedures*

One to several hours allowed recovery from anesthesia once the fish were put into the swimming tube with the air-lift circulation on. Additional time was required to train fish to swim steadily in the pump stream flow as velocities were changed. The most effective training method was to just slightly open the control valve with the pump running so that the fish drifted to the rear screen. Within 5 to 10 minutes, the fish would begin slow swimming to avoid tail flexion against the screen. Flow velocity was then slowly increased until the fish again stopped or began dart swimming or thrashing. When this happened, the pump was shut off and the animal given a brief rest lasting 5 to 10 minutes before another training period. Training was considered complete when the animal would maintain a relatively fixed position between front and back screens as the control valve was turned from off to full on and the reverse.

Once a fish was trained to sustain swimming over the complete velocity range of the apparatus, a routine procedure was followed. A rest period of about 10 minutes was allowed after each swimming bout. Transition velocities for ram ventilation were established in most cases by four swimming periods. The pump was turned on after a rest period and the control valve opened in stages to give flow velocities that approximated step increases of 5 to 10  $\text{cm} \cdot \text{sec}^{-1}$  flow velocity (manometer pressure equivalent) until the velocity maximum for the pump was reached. Sufficient time was allowed at each step to allow the manometer to stabilize and to obtain a 15 second polygraph record of cardiac and opercular cycles. The entire range of possible flow velocities with the fish swimming was covered in this way in about 10 minutes. Following the rest period, the sequence was repeated in reverse order. The reverse sequence was begun with the pump full on and then followed by step-wise reductions in pump flow until the pump was fully throttled, and the fish again at rest. One repeat usually sufficed unless excessive electronic noise or weak muscle signals made derivation of event rates from the polygraph record difficult.

## RESULTS

*Ram ventilation*

*Critical swimming velocity.* The transition to ram gill ventilation in fish is a graded process as swimming picks up from rest. The first indication that a critical swimming speed has been reached is signalled by the drop-out of single cycles. The drop-out continues until only occasional ventilatory movements and "coughs" are noticed. A graded series just following the training period for a bluefish is illustrated in Figure 2. Return of active movements with gradual reductions in swimming velocity to below critical shows nearly the same sequence, but in reverse order. Generally, subsequent swimming bouts with this and the other ram-ventilating species showed some decrease in the velocity critical for the transition to ram ventilation. In fact, transition speeds of experienced fish may fall to less than half that observed in initial tests so that switch-over to ram ventilation can occur at a surprisingly slow swimming speed. This contrast is best noted by comparison of the bluefish swimming bout given as Figure 2 and the transition range for all bluefish tested summarized in Table 11.

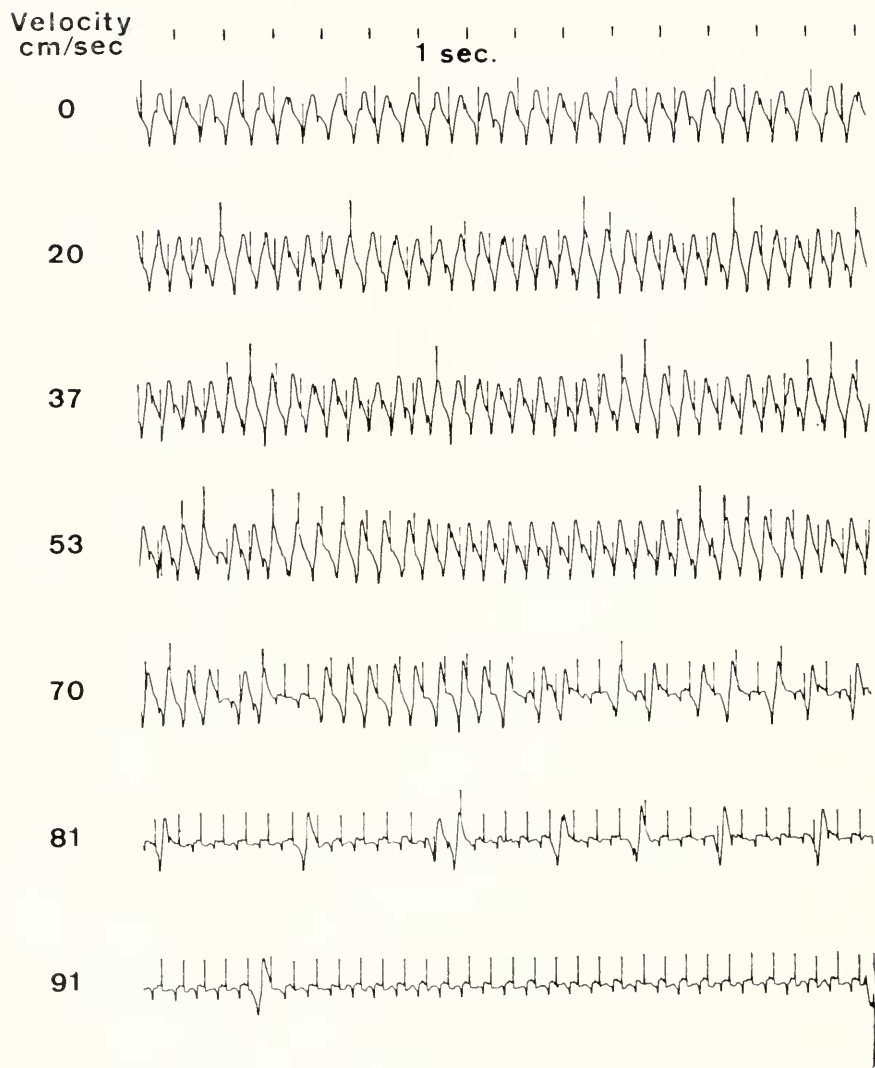


FIGURE 2. A combined sequence of EMG slow-wave components recorded from the *adductor mandibularis* muscle (left side) and the ECG of a bluefish during acceleration to and above a swimming speed sufficient to support ram gill ventilation. The time marks in this and subsequent figures denote 1-second intervals.

Although patterns for conversion to ram gill ventilation of different fish are similar, there does seem to be great variation between individuals in their behavioral selection of swimming velocities for switching ventilation modes. Figure 3 shows conversion patterns for each of the five mackerel used in the study (see also Heath, 1973). Clearly, the transition can be gradual or abrupt, and with or without a marked increase in the frequency of active respiratory movements prior to adoption of the ram mode.

TABLE II

*Mean values and ranges for opercular (O) and cardiac (C) rate changes in resting and active marine fishes*

Species (N)		Aquarium display cpm	Resting rate swimming tube cpm	Active rate at transition velocity cpm	Active rate at 90 cm $\cdot$ sec $^{-1}$	% change from rest		Swimming speed at transition cm $\cdot$ sec $^{-1}$
						At transition	At 90cm $\cdot$ sec $^{-1}$	
Mackerel (5)	O	—	124 (110-140)	134 (125-175)	—	8	—	67
	C	—	100 ( 72-133)	121 ( 89-140)	126 ( 98-140)	21	26	(53-75)
Blue runner (7)	O	—	80 ( 52-105)	119 ( 90-135)	—	49	—	48
	C	—	43 ( 26- 62)	62 ( 50- 92)	72 (57-105)	44	67	(35-75)
Bluefish (11)	O	77 (SD, $\pm$ 13)	99 ( 65-145)	138 (105-185)	—	39	—	69
	C	—	83 ( 52-115)	113 ( 92-160)	117 ( 98-160)	36	41	(49-82)
Northern scup (5)	O	51 (SD, $\pm$ 10)	148 (120-180)	196 (175-200)	—	32	—	66
	C	—	81 ( 54-105)	142 ( 80-150)	146 (130-160)	75	80	(44-79)
Mullet (4)	O	—	148 (113-180)	—	201 (130-232)	—	36	—
	C	—	104 ( 88-120)	—	124 (112-132)	—	19	—

Conversions to ram ventilation, the mullet excepted, were completed at velocities under 90 cm  $\cdot$ sec $^{-1}$  by all the fish tested. This is a swimming-speed equivalent of 2.7 to 4.7 BL  $\cdot$ sec $^{-1}$  (body lengths per second) according to the size of the mackerel used (Figs. 3 and 4). This range does not substantially exceed the open-sea cruising speed expected for mackerel of this size or roughly 2 BL  $\cdot$ sec $^{-1}$ , as based on Magnuson's estimates for speed minimums required to maintain hydrostatic equilibrium (1970). Table II gives similar ranges and mean values for complete adoption of ram ventilation by all of the species groups studied.

Individuals of all species tested occasionally stopped swimming at flow velocities that were above critical and drifted to the rear screen of the chamber. When this happened, ventilation movements most often reappeared immediately and continued until swimming was resumed. Two of the blue runners continued ram ventilation in several swimming bouts after drifting back to the rear screen. This unusual tactic was not observed in swimming bouts with the other marine species. Note also (Table II) that the average transition velocity for blue runners seems to be lower than for the other ram ventilators. A notable exception to be considered later, is the remora which ram ventilates attached to its swimming host, but only above velocities of about 1 km (Muir and Buckley, 1967).

None of the mullet showed signs of even partial conversion to ram ventilation during enforced swimming, despite the fact that they trained readily to steady swimming in the apparatus. These fish appeared to be in excellent health, but had all been captured and held in the aquarium at Woods Hole about 1 month prior to their use. All survived the swimming bouts for at least a month after electrode removal in one of the holding tanks. Figure 4 includes a typical record

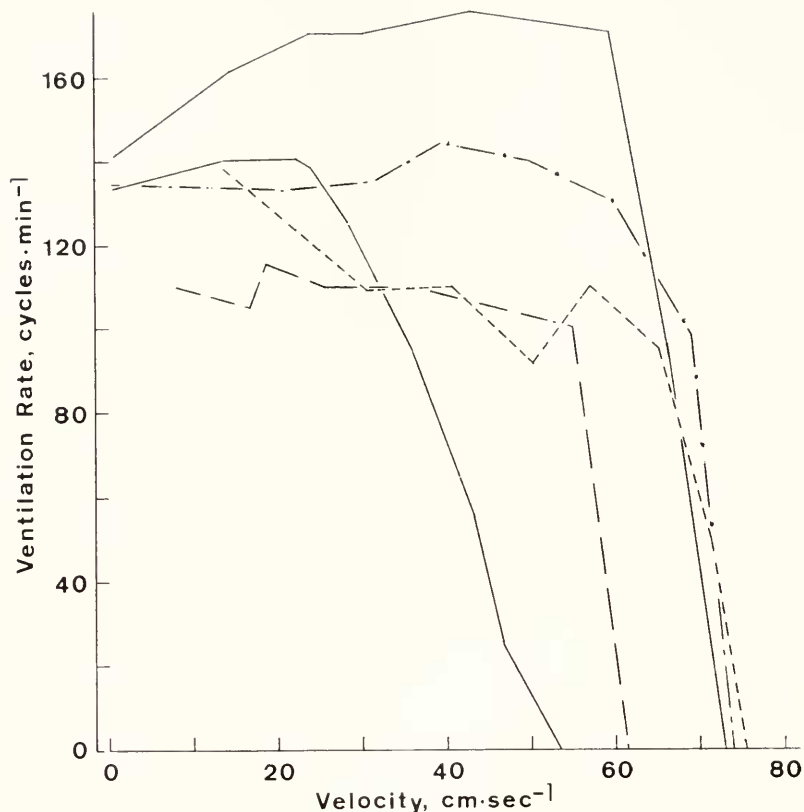


FIGURE 3. Active gill ventilation rates of five Atlantic mackerel (see Tables I and II) relative to enforced swimming speed. Rates were determined by counting all cyclic ventilatory movements that appeared on 30-second strips of polygraph record.

with a simultaneous display of tail beats obtained by proximity detection as the pump flow was valved from off to full-on to induce swimming at 85 to 90  $\text{cm}\cdot\text{sec}^{-1}$ . The records shown for the other species were obtained in a similar way by rapid valving of the pump output to produce swimming at speeds below and above the active to passive transitions in ventilation.

*Transition characteristics.* Figure 4 also demonstrates that timing differences are consistent between the onset of ram ventilation and return to active ventilation when swimming speeds are abruptly increased or decreased by manipulation of the pump flow. The return to active ventilation by most of the fish used generally was found to require less time than switching to the ram mode. Figure 5 contrasts in that conversions between ventilatory modes by this bluefish proved to be nearly equal in timing. The second, early return to active ventilation (Fig. 5, down arrow) most likely represents a single movement, seen to occur normally in some swimming bouts (Fig. 2, 91  $\text{cm}\cdot\text{sec}^{-1}$ ). Allowing for the chance occurrence of single respiratory movements and possible operational errors, a great

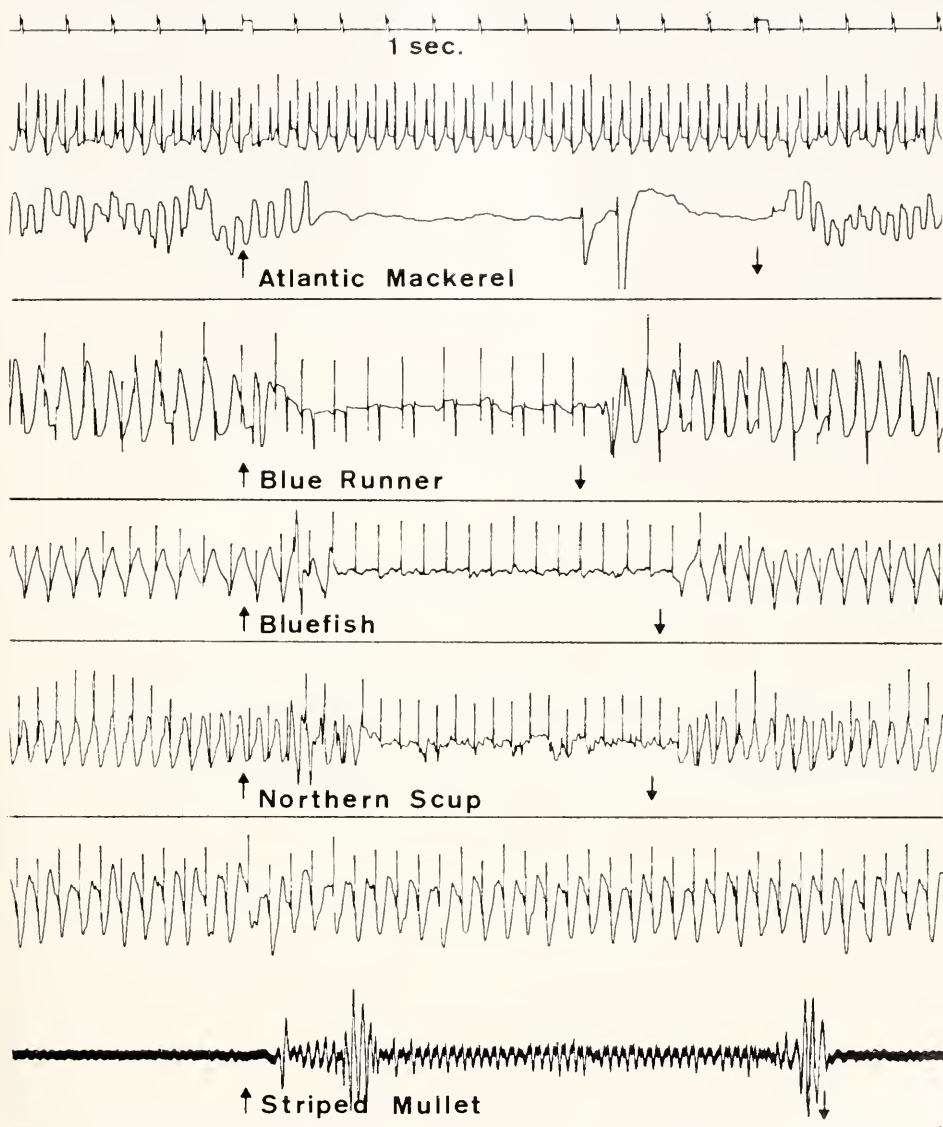


FIGURE 4. Active to passive transitions in gill ventilation of five marine species from rest to swimming just above transition velocities following turn-on (arrow up) and turn-off (arrow down) of the pump. The lower trace for the Atlantic mackerel is shown for clarity in separation of cardiac and ventilatory events. The lower record for the striped mullet represents tail-beat frequency recorded by proximity detection of the movement of *mu*-metal bands around the caudal fin peduncle. Changes in heart rates are slight due to the lack of rest periods prior to these sequences.



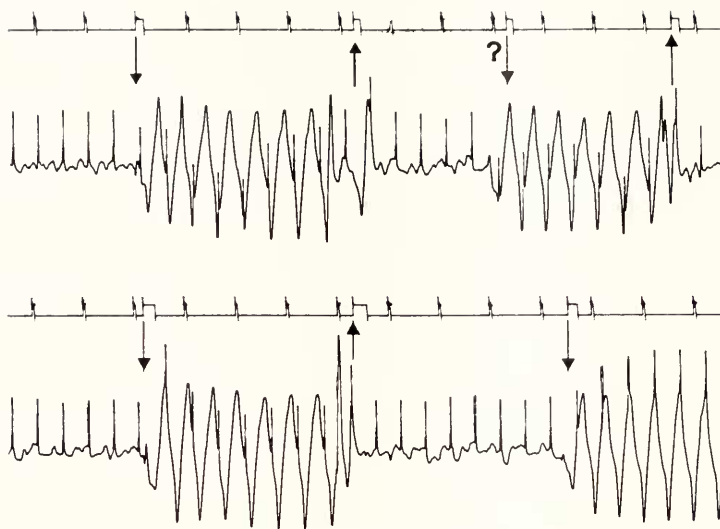


FIGURE 5. Repeated sequences of pump valving to vary swimming speeds of a bluefish from just above to just below velocities for conversion between active and passive modes of gill ventilation. Up and down arrows indicate respectively, decreasing and increasing pump flow.

number of switching-time measurements indicate that all of the ram ventilators can initiate active ventilation in as short a period as 0.2 second following sudden drops in the speed of water flow to below critical swimming rates for ram ventilation.

Usually the transition to the ram mode was marked by completion of at least one complete ventilatory cycle before actual ram gill ventilation began. Strong "coughs" were sometimes seen, both at the onset of ram ventilation, and preceding the return of rhythmic breathing, as swimming velocities were made to change above and below critical speeds for switching between modes. In other respects, the pattern of single ventilatory movements shows little change in amplitude or timing as swimming begins and the suppression of individual cycles occur with ram gill ventilation (Fig. 2).

#### *Frequency changes—branchial and cardiac pumps*

Gill ventilation rates of wired fish recorded before and after swimming bouts (30 minutes rest) all greatly exceed rates determined for inactive, undisturbed fish. For example, Table II lists rates for experimental bluefish and scup as well as rates for display fish at the aquarium at Woods Hole. The latter were recorded at 9 a.m. before public open hours (Logan and Roberts, unpublished observations; Roberts, 1974). Large differences such as these can be expected because handling fish elevates their metabolism and excitability for prolonged periods (Roberts, 1964; Muir and Buckley, 1967; Sutterlin, 1969; Spoor, Neihsel and Drummond, 1971). The same can be said for heart-beat rates although these were not recorded along with opercular frequencies of the display bluefish and scup.

Table II also shows that heart and ventilatory rates increase proportionally

with swimming velocity, although variability is large. Beyond the transition speed for conversion to ram ventilation, heart rates of all species increased with further increase in swimming speed. No obvious cardiac rate changes or alterations in ECG patterns were found associated with conversions between active and passive gill ventilation (Figs. 2, 4, and 5). Even at the higher swimming velocities, visual stimuli (shadows, movements of the operator) produced the well-known reflex bradycardia (Labat, 1966; Randall, 1970a; Roberts, 1973). Therefore, considerable reserve accommodation in cardiac function remains at moderate swimming velocities, and at speeds higher than necessary to support ram ventilation.

### DISCUSSION

In a sense it is surprising that the use of ram gill ventilation is widespread among fishes other than those known to be high-speed or continuous swimmers of open-water habit. Yet, if the supposition is correct that ventilatory efficiency improves with conversion from active to passive ventilation once swimming velocity reaches  $1.5 \text{ km sec}^{-1}$  (Brown and Muir, 1970) the advantage of conversion between stops for feeding or other fish activity becomes more obvious (Roberts, 1974).

There is a proviso, however. That is, successful ram ventilation seems to require that a fish be above a certain size so its normal cruising speed exceeds the velocity minimum for support of the passive ventilation mode. For example, it was mentioned above that scombrids have outgrown the capacity of their active branchial pump system so adult survival is dependent upon continuous swimming for a variety of reasons (Hall, 1930; Brown and Muir, 1970; Magnuson, 1970, 1973). Apparently the Atlantic mackerel, and most scombrids as well, lose the ability to ventilate the gills by rhythmic breathing as an ontogenetic development. Captive juvenile Atlantic mackerel ranging in body size from 2 to 12 cm actively ventilate their gills and often "stand dead in the water" (personal observations, aquarium, Woods Hole). Most likely, fish this small simply are not able to swim continuously at speeds fast enough to sustain ram ventilation.

Table III lists species known to utilize ram ventilation. It includes only two species from among the sharks and omits many probable ram ventilators from both major classes of fish only for the reason that many reports lack reasonable substantiation. The list is based upon careful visual, physiological and cinematographic monitoring. Brief comments on habitats were abstracted from the monographs of Bigelow and Schroeder (1953) and Miller and Lea (1972) for the coastal marine fishes of the Atlantic northeast and California, respectively. Common names and ordering of the families and species have followed the recommendations of the Committee on Names of Fishes, American Fisheries Society (1970).

Just as important is the fact that some fish do not ram ventilate at all. The mullet is a curious exception for it is an inshore, near surface high-speed swimmer. It has an unusually small mouth and feeds mostly on plankton and algae. Perhaps the mullet's active respiratory mode is somehow linked with its feeding style during swimming.

Demersal fish, notably those equipped with large branchiostegal baskets (see McAllister, 1968) probably do not convert to passive gill ventilation at any swim-

TABLE III  
*Ram ventilating fish*

Species and systematic position	Habitat	Method	Source
Chondrichthyes			
Odontaspidae			
<i>Odontaspis taurus</i> (sand tiger)	subtidal, beaches and bays	visual count, aquarium	Roberts (unpub- lished) von Wah- lert (1964)
Carcharhinidae			
<i>Triakis semifasciata</i> (leopard shark)	subtidal, beaches and bays	cinema photog- raphy, aquarium	Hughes (1960)
Osteichthyes			
Salmonidae			
<i>Onchorhynchus nerka</i> (sockeye salmon)	pelagic and mid- water, anadrom- ous	branchial pressures	Smith <i>et al</i> (1967)
<i>Salmo gairdneri</i> (rainbow trout)	fresh waters and anadromous	electromyograms	Roberts (unpub- lished)
Percichthyidae			
<i>Morone saxatilis</i> (striped bass)	near shore pelagic and fresh waters, anadromous	electromyograms	Roberts (this paper)
Echeneidae			
<i>Remora remora</i> (remora)	open ocean, surface to mid-water	cinema photog- graphy, water tunnel	Muir and Buckley (1967)
Pomatomidae			
<i>Pomatomus saltatrix</i> (bluefish)	near shore and bays, pelagic to mid- water	electromyograms	Roberts (this paper)
Carangidae			
<i>Caranx crysos</i> (blue runner)	near shore and bays, pelagic to mid- water	electromyograms	Roberts (this paper)
<i>Trachurus symmetricus</i> (jack mackerel)	near shore to open ocean, pelagic to mid-water	electromyograms	Roberts (unpub- lished)
Sparidae			
<i>Stenotomus chrysops</i> (scup)	demersal to mid- water	electromyograms	Roberts (this paper)
Kyphosidae			
<i>Medialuna californiensis</i> (halfmoon)	mid-water, kelp beds	electromyograms	Roberts (unpub- lished)
Scombridae			
<i>Katsuwonus pelamis</i> (skipjack tuna)	pelagic, open ocean	cinema photog- raphy (NMFS, Honolulu)	Brown and Muir (1970)
<i>Scomber japonicus</i> (Pacific mackerel)	near shore, pelagic	electromyograms	Roberts (unpub- lished)
<i>Scomber scombrus</i> (Atlantic mackerel)	near shore, pelagic	electromyograms	Roberts (this paper)

ming velocity. Their respiratory apparatus is well designed for respiration in standing water and functionally, the opercular pump dominates. About 90% of the respiratory cycle at rest is spent in slow opercular aspiration of water through the gills with the mouth open (Hughes, 1960a; Hughes and Roberts, 1969; Roberts, 1974). Consequently, respiration rates of these fish usually are considerably lower than their cardiac rates (Hughes, personal communication; Roberts, 1974). In fact, comparison of resting ventilation and cardiac frequencies serves as a "rule of thumb" to differentiate between fish that depend primarily upon the action of the opercular pump and fish in which branchial ventilation is equally shared by the buccal and opercular pumps. For these, rate ratios of about one can be expected. The latter pattern for propelling water across the gills generally prevails among fast swimmers of mid-water and pelagic habits. The fast swimmers usually are good ram ventilators as well.

For an example, the family Scorpaenidae can be cited. The family includes two major groups, the scorpionfish and the rockfish, *Sebastes*. All have well-developed branchiostegal rays and membranes. A number of the rockfish have evolved away from a strictly demersal existence. Some closely resemble the sea basses (Serranidae) of the genus *Paralabrax* in body form, development of the branchiostegal system and habits. None of these fish types so far examined ram ventilate (*P. clathratus*; *S. mystinus*, *serranoides*, *paucispinis*). Yet, with the exception of the blue rockfish, *S. mystinus*, all trained rapidly to enforced swimming at speeds well above the requirement for sustained ram ventilation.

Another fish, the anadromous striped bass, *Morone saxatilis* (Percichthyidae), sometimes included with the Serranidae (Miller and Lea, 1972), seems ready to adopt the ram mode of gill ventilation at a swimming speed of about 50 cm·sec<sup>-1</sup>. Only a single specimen was tested (total length, 46 cm). Unlike the serranids, however, the branchiostegals of the striped bass are much reduced and the cardiac-ventilatory rate ratio is about one.

Just as extensive development of the branchiostegal system facilitates respiration in quiet water, this development probably sets a limit to the speed at which fish can cruise routinely and still ensure reasonable energy expenditures for gill ventilation. Structural stability of the lightly-build branchiostegal rays and membranes, and the drag resistance they present when laterally expanded during swimming are important considerations. But as yet, no detailed hydrodynamic analyses exist to describe the array of niche compromises made during the evolution of modern fishes to meet the joint needs of respiratory gas exchange, and swimming for prey capture, migration, and reproduction.

Experimental verification that many swimming fish ram ventilate has been a relatively simple task. Providing the answers to why and how ram gill ventilation occurs has been more difficult. Of the two questions, the answer to why is the hardest to supply in satisfactory form at the present stage of investigations on fish energetics. A large part of the problem rests with assessing the efficiency of gill ventilation in swimming fish and hence, the work load of ventilation with respect to total body metabolism (see also Jones, 1971).

Estimates of energetic costs of active gill ventilation versus total metabolism in resting fish range from a low of 0.5% (Alexander, 1970) to as high as 43% (Schumann and Piiper, 1966). Jones calculations for a trout model (1971),

reveal a theoretical cost as small as 1%, despite assumption of a low resting efficiency for the operation of the branchial musculature in propelling water through the gills (3 to 4% efficiency). Intermediate cost estimates of 10% (Hughes, 1973) and 5 to 15% (Cameron and Cech, 1970) also have been suggested. However, the general accuracy of these estimates as applied to rhythmic gill ventilation is doubtful due to the complex hydrodynamic integration of changing flow rates and pressure profiles that occurs during single respiratory cycles (Hughes and Saunders, 1970; Ballintijn, 1972). The critical factors of environmental temperature and oxygen availability also must be considered for both exert strong influences upon ventilatory stroke volume, coupling of the branchial pumps, and hence upon respiratory efficiency (Hughes and Roberts, 1970; Hughes and Saunders, 1970; Heath and Hughes, 1973).

Respiratory energetics of sluggish demersal species that have elaborate branchiostegal systems scarcely are comparable with the energetics of pelagic, high-speed swimmers which have only remnants of branchiostegal rays and membranes. The energy cost of active ventilation for a bottom-living fish probably is high, but affordable. They often are opportunistic predators that swim in short darts to seize prey or swim slowly to feed on other sluggish bottom species. Midwater and pelagic fish contrast for they usually depend upon chasing down active prey or upon planktonic gathering and are more or less continuous swimmers. Their metabolic costs for gill ventilation also may be high during brief pauses in swimming, but the cost probably does not increase proportionately with total metabolism during swimming up to ram-ventilating speeds. The reason is that when a fish begins to swim, its forward motion causes pressure to rise at the mouth, partially relieving power requirements for the buccal fore-pump (Hughes, 1960a; Hughes and Shelton, 1962; Cameron and Cech, 1970). Opercular aspiration also may be facilitated by the venturi effect as water streaming along the body passes the gill-cover margins in spite of some drag losses due to cyclic abductions of the opercular doors (also see Brown and Muir, 1970).

Further acceleration to a ram speed results in a graded transfer of the metabolic cost of rhythmic ventilatory movements to the drag forces of swimming (Brown and Muir, 1970). Some lesser amount of energy must be reserved for tonic holding of the mouth gape and the opercular exit slots to sizes suitable for respiratory needs once the conversion to ram gill ventilation is complete. Thus, the switch-over from active to passive gill ventilation is a tactic that probably saves considerable energy. However, not all of the savings result simply from the transfer of respiratory work from one set of muscles to another. Loss in locomotory efficiency is also a probable consequence of rhythmic gill ventilation, especially at high speeds. For example, cyclic variations occur in the cross-sectional area of the head as the opercular doors open and close. Changes in mouth gape also occur with operation of the buccal phase of branchial pumping. Such drag oscillations are likely as well to generate periodic turbulence, adding still further to the work load of swimming. Little is known about these factors and their effects on swimming. But, the available evidence shows that the events of gill ventilation and of swimming must be tightly coupled by unavoidable hydrodynamic interactions. The same should be true of their relative metabolic efficiencies.



Only a single study has been directed toward assessment of the work load during ram gill ventilation. Brown and Muir (1970) have calculated the ventilation drag-resistance of a 44-cm skipjack tuna (*K. pelamis*) swimming at a basal speed of  $66 \text{ cm} \cdot \text{sec}^{-1}$  to be about 7% of the total body drag. Translation of the drag forces into metabolic expenditures for swimming and other functions, has led them to estimate the cost of ram ventilation for a tuna swimming at basal speed to range from 1 to 3% of total metabolism—a cost much lower than most prior estimates for active ventilation in non-swimming fish.

Aside from the fact that ram gill ventilation is used by most active fish that have been tested (Table III), one unusual example also attests to the efficacy of the ram mode. The small shark sucker (*R. remora*) normally is a sluggish swimmer that uses active ventilation. Yet when this fish attaches to a passing shark or other large swimming host, it too can adopt the ram mode when the host reaches the requisite speed. In a sense, they gain a “free ride” by transferring the work load of gill ventilation to their hosts. But, they seem to do it by using neural adaptations for ram ventilation that most likely are ancestral to the adaptations which permit their form of locomotory and feeding commensalism (Table III). Muir and Buckley (1967) have found that remoras placed in a water tunnel would attach to the wall as flow velocities through the tunnel reached 20 to  $30 \text{ cm} \cdot \text{sec}^{-1}$ . Switch-over from active to passive gill ventilation was found to range from 50 to  $80 \text{ cm} \cdot \text{sec}^{-1}$ . This is a range remarkably similar to the transition velocities reported here for other marine species (Table II).

The work expended by a species in ventilating its gills between a dead stop and a burst of maximal swimming must represent a compromise with costs of other activities as defined by its niche and physical factors in its habitat. Ultimately, as Brett has shown (1964) for the sockeye salmon (*O. nerka*), the maximal sustainable swimming speed of a fish will be limited by the cost of gill ventilation, and its ability to manage an oxygen debt, combined with the costs of cardiac pumping as Jones suggests (1971). This means that routine levels of activity in swimming, feeding, and ventilating the gills will represent partitioning of energy available for these functions according to a fish's life style whether it is benthic or pelagic, and whether it is a sluggish swimmer or a very active one. If Jones' (1971) and Brown and Muir's (1970) attempts to model ventilatory energetics are reasonable, the costs of gill ventilation for active fish that ram ventilate may remain as low as 1 to 3% of total metabolism over a wide range of swimming speeds.

What speed might mark an upper limit for a good swimmer is difficult to estimate, but it is probably not less than cruising velocities for most pelagic species. Very likely another factor becomes significant at still higher speeds or during burst swimming. A fall in the %-utilization of oxygen from the respiratory stream should occur as the ventilatory minute-volume increases with increasing metabolic needs (Hughes, 1966; Randall, 1970b; Hughes and Morgan, 1973). This represents a loss in respiratory efficiency that would be additive to the work load of swimming.

Much could be learned to substantiate their trout and skipjack estimates by use of water or wind tunnel models. In fact, the brancial system of fish respiring in the ram mode resembles, in an engineering sense, the design of a combined

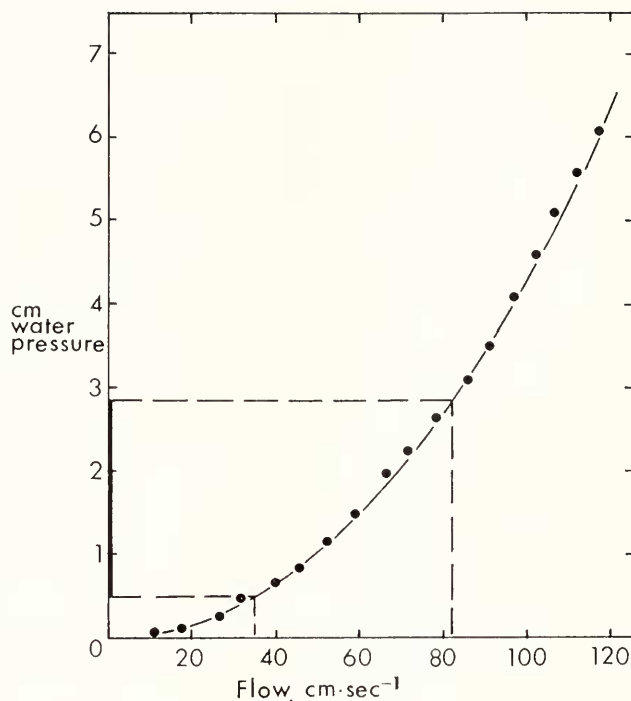


FIGURE 6. Secondary calibration of a Blažka swimming tunnel (respirometer type) with a combined impact-reverse pitot tube in the axial flow of the swimming chamber to give pressure equivalents of flow velocity in centimeters of water. The primary calibration was obtained by use of a ducted, impeller flow-meter (Marine Advisers Inc., La Jolla, California; model B-7C). Minimal and maximal estimates for across-gill differential pressures have been extrapolated on the ordinate according to the range of swimming speeds permitting ram gill ventilation for the fishes listed in Table II.

impact-reverse pitot tube with variable up- and downstream orifices. The comparison has limits. The pitot tube typically is a zero-flow pressure measuring device so the resistance between orifices is infinite. The branchial system differs in that through-flow occurs as a volume rate determined primarily by the resistivity of the gill screen. Figure 6 illustrates the pressure differential developed between impact and reverse openings of a pitot tube located in a "swimming" respirometer of the Blažka type (loaned by Dr. F. E. J. Fry, University of Toronto) relative to water flow velocities from 0 to 120  $\text{cm}\cdot\text{sec}^{-1}$ . The extrapolated buccal-post branchial pressure range also is shown (ordinate). This range of pressure differences corresponds to minimal and maximal swimming speeds for ram gill ventilation by the fish species listed in Table II (*i.e.*, blue runner and bluefish, respectively). Assuming that a resemblance to the combined impact-reverse pitot is reasonable, then an across-gill pressure drop as low as 0.5 cm enables some fish to swim as slowly as 35  $\text{cm}\cdot\text{sec}^{-1}$  and still support ram gill ventilation.

Muir and Buckley (1967) have determined via buccal and opercular cannulas that the average pressure necessary to force water through the gills of actively

breathing remoras is 0.87 cm. Yet, these investigators have estimated that the passive mode of ventilation in swimming remoras requires an across-gill pressure drop of 1.87 cm water pressure. The latter figure probably is too high for a minimal value for it was based on the use of a simple impact pitot that does not correct for static pressures generated in the positive-pressure pumping system they employed. However, if the minimal swimming speed for conversion to ram ventilation by a remora is selected (page 583,  $50 \text{ cm} \cdot \text{sec}^{-1}$ , Muir and Buckley, 1967), and the curve in Figure 6 is used, a differential of just over 1 cm water pressure results. Therefore, when an allowance is made for inertial losses that must occur with branchial flow-rate changes during active as opposed to passive gill ventilation, the suggested minimal value of a 0.5 cm differential pressure to support ram gill ventilation seems acceptable.

The transition to ram ventilation from active gill ventilation in swimming teleosts superficially resembles breath holding in man and diving aerial-breathers among vertebrates. It is marked by cessation of rhythmic breathing and seems not to be mediated by chemoreceptive detection of changes in the concentration of respiratory gases or pH. Recent experiments to be reported elsewhere, indicate that the transition swimming velocity for ram ventilation is only slightly increased by warming ( $1^{\circ} \text{ C}$  per minute; bluefish, blue runners) or by dropping the  $\text{pO}_2$  in a swimming tunnel (halfmoons, jack mackerel), and then only at extremes.

Active ventilation in resting fish is driven by the combined actions of the buccal and opercular pumps; effected by contractions in antagonistic arrangements of the branchial musculature (Ballintijn and Hughes, 1965; Ballintijn, 1972). Pressure generated by streaming flow at the mouth allows transfer of much of the ventilatory work to the swimming musculature as the transition swimming speed for ram ventilation modes is accomplished by reflex conversion of motor outputs from the medullary respiratory areas of the CNS from a cyclic to a tonic drive of the branchial muscles.

The fact that tonic control of the buccal musculature is maintained during ram gill ventilation has been verified for a mackerel by Brown and Muir (1970). They found that progressive reductions in the  $\text{pO}_2$  of water circulating in a water-tunnel respirometer results in graded increases in mouth gape at fixed swimming speeds. Furthermore, the mouth of an anesthetized fish usually is forced fully open or fully closed in the stream flow of a swimming tunnel, depending upon the streamline shape of the head and the degree of mouth gape when the flow is started. Clearly, mouth gape opening is not a passive process in swimming fish that do ram ventilate.

Despite the large effort that has been spent on the examination of adaptive respiratory reflexes in fish, specific receptors for initiating reflex action have not been identified. However, it is known that proprioceptive elements sensitive to gill filament displacement are located in the gill arches (Sutterlin and Saunders, 1969). Pertinent to this discussion are receptors for monitoring water flow velocity, and muscular activity effecting ventilation and swimming.

Delay in the return of active gill ventilation is so short in a ram ventilating fish when swimming slows or stops, that reflex switching by way of oxygen sampling is unlikely for this event (Figs. 4, 5). Return of rhythmic breathing in bluefish and blue runners can occur within 0.3 second of flow shut-down in a

swimming tunnel. Timing in the blocking of rhythmic movements as swimming begins at speeds above the transition speed for ram gill ventilation is a different case. Several seconds may elapse before a fish begins to ram ventilate, but during this time there will not have been any interruption of the branchial water flow.

Receptor systems subject only to minor influences by metabolic loading or by temperature change would seem to provide the most reliable cues for switching between ventilatory modes. Mechanoreceptors sensitive to water flow velocity such as elements of the acoustico-lateralis system, and proprioceptors in the gill arches and the swimming musculature (stretch receptors) are likely candidates for this function. Monitoring of water flow velocity over the body and through the branchial chambers, and the detection of tail-beat frequency should be influenced only by the properties of water as a flowing fluid (see Hughes and Roberts, 1970; Randall, 1970b). Consequently, the thermal error in receptor functioning should be negligible for fish swimming at set velocities over the temperature range of their usual habitats.

Although both receptor detection of water-flow rates and events in swimming may be critical for reflex conversion to ram gill ventilation as reported above, some exceptions have been noted. Two of the blue runners from the group listed in Table II were found to continue ram gill ventilation after drifting to the rear screen of the swimming apparatus during swimming bouts. No obvious signs of fatigue were observed when they quit swimming. Under the unnatural circumstances of forced holding of these fish in a stream flow, it is possible that conditioning occurred that permitted continuation of the ram mode. A similar explanation might be applied to the ram gill ventilation of remoras attached to the wall of a swimming tunnel. However, Muir and Buckley (1967, page 582) also have reported that the swimming musculature becomes relaxed when the flow reaches ram ventilating speeds so that the body "... often swayed with the current." Assuming that proprioceptive return is critical to reflex control of ram ventilation in the remora as well, stretch receptor systems still could be activated by passive tail oscillations at frequencies dependent upon water flow velocity.

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#### SUMMARY

1. Characteristics of cyclic breathing movements have been examined in a number of fish species at rest and during swimming acceleration to velocities



above those sufficient to induce transfers from active to passive gill ventilation (ram gill ventilation). They were trained to swim in one of several types of swimming tunnels after electrode implants to permit recording of ECG's and ventilatory muscle EMG's.

2. Transfer to the ram mode of gill breathing is marked by a drop-out of individual cyclic breathing movements as swimming increases from rest. When the swimming speed reaches about  $65 \text{ cm} \cdot \text{sec}^{-1}$ , most fish that use ram gill ventilation complete conversion to the ram mode ( $35$  to  $82 \text{ cm} \cdot \text{sec}^{-1}$ , range of all fish tested). This is equivalent to an across-gill differential pressure of  $2.1 \text{ cm H}_2\text{O}$  as measured with a combined impact-reverse pitot tube as an approximate model. Generally, a fish must be swimming to ram gill ventilate, but some exceptions are noted such as the shark-riding remoras.

3. Control of the transfer between gill ventilation modes appears basically to be a reflex shut-down of rhythmic breathing initiated by mechanoreceptive detection of water flow-velocity and the detection of swimming movements. Reflex transitions between active and passive breathing seem to happen too rapidly for a sufficient change of respiratory gas concentrations to occur and allow triggering of chemoreceptors.

4. No unusual events are detectable in the ECG's of swimming fish as they reach and surpass speeds sufficient to maintain the ram mode. Cardioacceleration varies as between sluggish and active swimmers, but seems to be independent of the mode of gill ventilation used.

5. Generally, demersal fishes that depend mainly upon the opercular phase for active gill ventilation, strongly aided by a well-developed branchiostegal system, do not ram ventilate. Conversely, nearly all species in which the work share of active ventilation is about equally buccal and opercular, probably use ram gill ventilation when they reach the requisite swimming speed. These are mostly mid-water to pelagic in habits so for them, transfer of the muscular work of gill ventilation from the branchial to the swimming musculature seems to serve a dual function—a reduction in the cost of breathing, and an improvement in swimming efficiency.

#### NOTE ADDED IN PROOF

Jones and Schwarzfeld (1974, *Resp. Physiol.*, **21**: 241–254) have revised Jones' earlier estimate (1971) for the oxygen cost of breathing to total metabolism in rainbow trout upward from one to ten per cent on the basis of measurements with hatchery fish.

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